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NATAL PARKS, GAME AND FISH
PRESERVATION BOARD.

Physical barriers and
the dispersion of freshwater
fish with particular reference
to Natal

A successful species extends its geographic range until a change in the environment prevents further dispersion. If the change is abrupt and clearly defined, such as that from dry land to water, it may be described as a physical barrier. An environmental transition of a more gradual nature, such as that associated with a decrease in temperature, forms a zone of ecological limitation. Physical barriers prevent animals reaching new territory whereas changing ecological factors make conditions unsuitable for the survival of species in areas that are accessible to individuals.

Barriers are of great importance zoogeographically, since isolation is a pre-requisite for faunal differentiation, but often an explanation for distributional patterns must be sought in the study of ecology. There is, indeed no fundamental distinction between physical barriers and ecological factors which limit dispersion. The sea is a physical barrier for terrestrial animals although its effectiveness varies according to an organism's structure and habits, and it is also a barrier for strictly freshwater fish. But if a fish has the necessary physiological adaptability it can move freely from fresh to salt water. While forming a definite physical barrier for some groups of organisms, the sea may have only an ecological influence on the distribution of others.

Faunistic changes which are correlated with local variations in topography and climate are of little or no significance to the zoogeographer. He is looking for broader patterns and delegates to the ecologist the task of correlating small scale variations in distribution with the mosaic of different habitats. Factors which are important ecologically may, however, be equally important zoogeographically.

Maximum and minimum temperature, for instance, vary from place to place within a limited area and often have a critical effect on the ecological balance. Latitudinal changes in temperature are highly significant to the zoogeographer, as shown by Poynton (1961) in relation to amphibian distribution in South Africa, and zonal temperature has undoubtedly played an important part in moulding the distribution patterns of many types of organisms.

It seems clear, therefore, that an ecological factor becomes zoogeographically significant if it limits or modifies patterns of distribution on an extensive scale. One of the main difficulties in utilizing factors such as temperature for the delimitation of zoogeographic regions, however, is to decide on a definite cartographical line of demarcation that corresponds with a significant change in the factor under consideration. No such difficulty occurs in discussing the effect of physical barriers, especially when dealing with a group such as freshwater fish

whose dispersion is curtailed by the sea, by divides between river systems and by waterfalls. The effect of these physical barriers is particularly noticeable on the eastern side of southern Africa between about 26° and 31° south latitude. Indeed the most remarkable point about the distribution of freshwater fish in that region is not that many species have failed to reach the more southerly rivers, but rather that some of them have overcome the barriers that lay in their path.

If a fish is to colonize new waters it must be able to swim there. Individual fish or fish eggs may possibly be transported by birds or by whirlwinds, but such factors are of negligible importance in the dispersion of a species. Human agency has played a part in the dispersion of certain fishes, but in general freshwater connections must be assumed to have existed wherever fish have spread from one body of fresh water to another. To reconcile this assumption with the observed discontinuity in the present habitats of many species requires the further assumption that past physiographic changes must have enabled fish to cross obstacles which are now impassable. The geomorphological history of a region provides clues to the nature of such physiographic changes.

No fossils of freshwater fish have been reported from south-east Africa, due perhaps to the recent origin of the fish fauna of Natal and the adjoining areas. Few endemic species occur and it appears probable that invasion of Natal rivers has taken place since the late Pliocene or early Pleistocene period when large scale tectonic movements occurred along the eastern edge of the African continent. In India a fauna which resembles that of south-eastern Africa in the absence of local specific differentiation is considered by Hora (1953) to have invaded its present habitat during the Pleistocene.

The criterion of taxonomic differentiation is, on its own, unreliable for estimating the age of a fauna since the rate of speciation may vary widely according to circumstances. Thus numerous endemic species of Cichlidae have evolved in Lake Victoria within a few hundred thousand years, whereas in other places species have remained unchanged for much longer periods. Brooks (1950) mentions the occurrence of two cyprinids, *Laabeo weeksi* and *Barbus eutaenia*, in an affluent of Lake Tanganyika. He suggests that both species inhabited the river before the formation of the lake and that no differentiation has taken place in the comparatively stable environment despite isolation since the late Pliocene. The specific identity of populations isolated in different Natal river systems does not, therefore, given any accurate guide to their antiquity although it seems clear that such populations cannot be as old as those of the south-western Cape where each river system has its own endemic species.

Possibly the earliest freshwater fish to reach Natal rivers did so through capture of tributaries of the Orange River system by eastward flowing rivers. A large species of *Laabeo* found only in the Tugela River is closely related to *Laabeo capensis* of the Orange River system, and its origin appears to have been due to catchment exchange. Another endemic *Laabeo*, which resembles the Orange River *L. umbratus*, presumably had a similar derivation. The dispersion of a very widespread minnow, *Barbus anoplus*, that occurs in many localities from the eastern Transvaal to the Gouritz and Olifants rivers in the Cape, may have been aided by catchment exchange. With the exception of these three species, however, there is no indication of any movement of fish from the interior plateau to Natal although a number of river captures took place in fairly recent geological times. One of the best known piracies was the diversion of the Slang River, which originally flowed into the Vaal-Orange system, but now forms the source of the Buffalo River and hence, part of the Tugela system. The capture of the Slang took place during the Pliocene period and should have resulted in a transfer of fish species from the Orange to the Tugela had the fish been present at the time of capture. In fact, however, the Slang contains only *Barbus anoplus*. The characteristic Orange River forms are all absent from the Slang and the large *Barbus* and *Laabeo* of the Tugela have been denied access by waterfalls.

The significance of waterfalls in limiting dispersion will be considered later, but first we must attempt to explain how the bulk of the fish fauna reached the waters in which they occur today. There is no difficulty in understanding how fish have moved from the Zambezi southwards to the Usutu-Pongolo system. Apart from the possibility that the Zambezi may at one time have flowed southwards to enter Delagoa Bay, sporadic flooding of the Mozambique plain could have enabled fish to swim from one river to another. The occurrence of many Zambezi species as far south as the Pongolo gives support to the assumption that a migration route has at times been available.

Seventeen of the Pongolo species are, however, absent from the rivers that flow across the Zululand coast plain and another four of the Pongolo species fail to reach the Tugela River, although low-lying land near the sea seems to offer the possibility of intermittent connection between different rivers. South of the Tugela the rivers are deeply entrenched in a terrain of high relief and debouch onto a narrow strip of low-lying coast before entering the sea. The number of species decreases southwards, but a few fishes are found in all Natal rivers. Beyond the Natal-Cape border the Umzimvubu River system is populated only by *Barbus anoplus*, a species which has a remarkably wide distribution from the Incomati River system in the northeast to the Gouritz River in the southwest.

The majority of Natal species whose range extends into the Province from farther north probably moved from river to river along the coast. Exchange of tributary streams between neighbouring river systems may have had some effect in aiding the movement of fish from one system to another. Tributary streams entering a river from the north have steeper courses, in general, than those entering from the south and might, therefore, incise more rapidly and so capture a neighbouring stream flowing in the opposite direction. The reason for the steeper gradient of northern tributaries is that the north side of an east flowing river valley is usually steeper than the south side, due to the effect of aspect on the rate of erosion. There is no evidence, however, that catchment exchange between Natal river systems has played a part in the dispersion of fish.

There is no conclusive evidence of any freshwater connections between Natal rivers, but there is a reasonable probability that such connections did exist at times through lagoons close to the sea. At the present time rivers tend to form lagoons behind the sand dunes that run parallel with the beach along the Natal coast. Each river tends to have its own lagoon, separate from those of its neighbours, but coastal dunes are subject to considerable variation, and the formation of a long continuous dune that temporarily blocked the mouths of several neighbouring rivers might create a body of fresh or slightly saline water connecting the different rivers. Within historical times the Umgeni, Umlaas, Isipingo and Umbogintwini rivers all flowed into Durban Bay. Very considerable fluctuations in the relative levels of land and sea occurred during the Pleistocene period and at certain stages the damming up of river mouths behind coastal dunes, built up by the sea, might have brought about the coalescence of individual lagoons.

The likelihood that fish reached Natal rivers along the coast is borne out by the occurrence of such dominant species as *Barbus natalensis* in the lower reaches of all the rivers, as far south as the Umtamvuna. They are found upstream towards the headwaters, except where waterfalls have prevented the ascent of a river. But now we find a very interesting phenomenon: certain waterfalls have had no apparent effect on dispersion whereas others have formed an insurmountable barrier.

The explanation for this anomaly is to be found in the geomorphological history of the region. King and King (1959) postulate a mighty upwarping that raised the land along an axis parallel to and not far from the Drakensberg escarpment. This large scale movement took place at the end of the Pliocene or early in the Pleistocene and resulted in a steepening of the courses of all the Natal Rivers. The increased gradient caused accelerated erosion and the

formation of the deeply incised valleys so characteristic of the landscape as we see it today. As the rivers cut downwards they encountered some rock formations that were harder than others. Dolerite is particularly resistant and wherever a sill or dyke of this rock crossed the course of a stream a waterfall developed. At the present day such falls may be of very considerable height; the Howick Falls, for example, on the Umgeni River are 311 ft. high. Yet these and other similar falls in the Natal midlands have not prevented *Barbus natalensis* from reaching sections of river farther upstream. The only reasonable conclusion is that the falls were not sufficiently well developed at the time of invasion of the rivers to form a barrier to upstream movement of the fish. Too many falls are involved to explain the presence of fish upstream by suggesting that transfer was effected by human or other adventitious agency.

Falls that occur at over 4,000 ft. altitude, towards the foot of the Drakensberg, have, in contrast to those lower down, acted as complete barriers to upstream movement of fish. This applies even on rivers where a considerable length of water suitable for *Barbus natalensis* occurs above the falls. Another point is that some of these barrier falls are not more than 15 or 20 ft. high. They are, however, situated above those sections of river which were affected by the Pleistocene steepening of the gradient. They have therefore presumably been in existence considerably longer than the far more impressive falls at lower elevations. Their greater age would account for their more significant effect as barriers to the dispersion of fish. In other parts of Africa the importance of waterfalls is well known. To mention only a few, the Semliki Falls, the Murchison Falls, the Murchison Rapids on the Shire and the Chibirra Falls on the Sabi have all had a marked influence on fish distribution by preventing access to the rivers above the falls.

The time of colonization of Natal rivers by *Barbus natalensis* and other widespread species was most probably early in the Pleistocene, when tectonic movements may have produced a temporary route along the coast, and before the waterfalls that interrupt the lower and middle courses of the rivers today had become established. The fact that many species which occur on Natal's northern border have not reached the more southerly rivers is easily explained if they are considered as representatives of later waves of migration. That explanation may not, of course, always be the correct one. Ecological requirements may enter the picture and also some species have better powers of dispersion than others.

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DISCUSSION

Mr. Stuckenberg: With regard to waterfalls as barriers, I am not altogether satisfied about the large Pliocene uplift postulated by King. Other authors are generally agreed that there were at least three major uplifts during the Tertiary. The effects of this particular uplift and the dating of Natal fish populations do not seem to my mind to be well established.

Prof. Balinsky: I have an uneasy feeling that the picture presented here is incomplete. It is taken for granted that most or all of these fish have migrated from thousands of miles away; but surely there were fish in Natal earlier than the Pleistocene. They are an old group. Unless there is some reason for thinking that there were no fish earlier than this period or that conditions in the region were untenable for fish, we must look upon this presentation with some doubt as the rivers are also very old.